Some special phylogenetic Adaptations in Lichens.—I.

BY ALBERT SCHNEIDER.

In a previous paper* I endeavored to show why lichens should be considered as a distinct class of plants. It is my purpose in this paper to discuss briefly some of the special adaptive features which these plants have acquired since their phylogeny as lichens. I shall preface this discussion with a few introductory statements.

Everywhere we can observe a balanced relationship between living organisms and their environment. All structures, no matter where they may occur, or what form they may assume, serve a definite purpose and perform a definite function. In many instances the structural conformations are so "rudimentary" and "imperfect" that we are unable to recognize their physiological significance. It is however unscientific to say that such structures perform no function, because we are unable to recognize a function. It were much more consistent to admit our ignorance and await further investigations, which may clear up some of the difficulties. I make these preliminary statements with special reference to lichens, because many of their structural adaptations have as yet not been satisfactorily explained. I also wish to call attention to the importance and special biologic significance of the tendency among modern scientific botanists to point out the interrelation of structure and function. There is no function without structure: without structure there could be no function.

From this it becomes evident that morphological and physiological investigations must go hand in hand. If we neglect one for the other we fall into a dangerous error, dangerous to the progress of biological science. The time is fortunately slowly passing away when morphology (usually external morphology) alone constitutes the science of life. The herbalists who go into wild ecstacies over having "discovered" a "new species" are slowly giving way to the scientists who are solving or endeavoring to solve some difficult life-problem. The fact that many scientific efforts are fruitless in direct results is not a reason for becoming

* The Biological Status of Lichens. BULLETIN, 22: 189–198. 1895.

discouraged; much less a reason why old fashioned "empiricists" should gloat over these failures and make strenuous efforts to perpetuate the old regime.

The knowledge gained from a purely morphological study of lichens, is in itself of little practical value if we can not find the correlated physiological interpretation. The scientific study of lichens is of very recent origin. Our knowledge of the physiology of these plants is especially deficient. Sufficient is, however, known in a general way, to enable us to give fairly accurate hypothetical physiological interpretations of most of the anatomical structures.

It is perfectly consistent to suppose that the lichen, during phylogenetic history, has undergone great adaptive changes. This statement is axiomatic and requires no further elucidation. From the nature of things it is also evident that the thallus has undergone the greatest adaptive changes.

As has been known for some time, the thallus in particular performs the function of assimilation, due to the presence of the symbiotic algae. Within recent years, Jumelle* has made a special study of chlorophyllian assimilation in lichens. The special structural adaptations which we are about to discuss are due to the fact that the fungal symbiont, which is incapable of assimilating CO_2, must make suitable concessions to the position and arrangement to the algal symbiont. This we find to be the case. In this paper I shall devote myself to foliaceous thalli and shall briefly consider some of the typical structures met with in such thalli; namely, the epidermal layer, the upper cortical layer, the algal ("gonidial") layer, the medullary layer, the lower cortical layer and the rhizoids. A typical epidermal layer is not present in all foliaceous lichens. It is, however, well developed in *Sticta* and *Stictina*. It consists of hyphal cells, two or three layers in thickness. The cells are placed horizontally and are very closely crowded, thus forming a protection against excessive evaporation. It serves a function similar to the epidermis in higher plants. In the genus *Leptogium* the epidermis consists of a single layer of cells presenting a close resem-

*Jumalle H. Recherches Physiologiques sur les Lichens. Revue generale de Botanique, 4: 49–64, 103–121, 159–175, 220–231, 259–272, 305–320. 1892.

blance to the cuticle of higher plants. We find a similar cuticular covering in the related genera, *Mallotium*, *Hydrothyria* and *Polychidium*. This structure not only serves the function of an epidermal layer, that is, prevents excessive evaporation, but also a mechanical function, giving greater firmness to the thallus. In other words, the single layer of cells in the above genera of the Collemaceae serves a function similar to the many-layered epidermis and cortical structure in *Sticta*, *Stictina* and other genera.

The epidermal layer is generally colored, usually a yellowish brown or dark brown. This is no doubt for the purpose of tempering the influence of sunlight. We may safely assume that the epidermal layer serves three functions. Its primary function is to prevent the excessive evaporation of moisture; its secondary functions are to reduce the injurious effect that direct isolation would have upon the symbiotic algae and to aid in protecting the underlying tissues as well as to give additional firmness to the thallus.* Below the epidermis is found the cortical layer, which is usually of considerable thickness in the majority of foliaceous lichens. I will not dwell upon its anatomical structure, as that is sufficiently well known. Its primary function is mechanical. It also serves a function similar to that of the epidermis; it prevents the evaporation of moisture.

According to the principles of mechanics and for the purpose of protection the cortical layer should occur near the upper surface of the thallus. But for physiological reasons the algal layer should also be near the upper surface, that the algae may be acted upon by the sunlight and that they may more readily come in contact with the CO_2 of the atmosphere and that they may readily give up the O which is liberated as the result of assimilation. We actually find such an adaptive relationship between the algal layer and the cortical layer. In many of the foliaceous lichens we find that the algae extend almost to the upper surface of certain circumscribed areas; that is the cortical layer is not of uniform thickness. Such an arrangement enables the algae to take up CO_2 from the atmosphere in exchange for the O

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* It should be borne in mind that there is no living structure whose function is purely mechanical or purely physiological. "Dead" structures *may* have only a mechanical function.

liberated. This could, however, not take place, if the epidermis and the upper and lower cortical layers were unbroken or without intercellular spaces. I shall now discuss some of the structural adaptations to meet this requirement.

On the closer examination of a thin vertical section of the thallus, it is found that in many of the foliaceous lichens numerous *intercellular* canals (intercellular spaces) pass from the algal layer through the cortical and epidermal layers. These canals, which resemble the stomata in their physiological function, facilitate the interchange of the gases resulting from the activities of chlorophyllian assimilation. The canals (breathing pores) are much branched and occur most frequently in the thin areas of the upper cortical layer. As a rule, they do not pass to the exterior in a vertical direction. In the epidermal layer they take almost a horizontal course; this is because the cells of the epidermis are elongated horizontally.

In the dry state these canals are practically closed, thus reducing the loss of moisture to a minimum. In the moist state they enlarge considerably, thus enabling assimilation, which is dependent upon the presence of CO_2 and sunlight, to take place. These breathing pores are especially numerous in *Nephromium*, *Solorina* and *Parmelia*.

Other lichen genera do not have the breathing pores just mentioned. For example they are not noticable in the genera *Sticta* and *Stictina*. In these two genera the epidermal layer is distinct, as has been stated. The upper cortical layer is of uniform thickness and consists of very compact, rather small hyphal cells. The lower cortical layer is comparatively thin and its cells are less closely united; yet they are sufficiently compact that no intercellular spaces can be detected. The question now arises, how are the enclosed algae * supplied with the necessary atmosphere? In my opinion this is done by means of the so-called *cyphellae* which occur on the lower surface of the thallus. These structures have long been known to lichenologists. Haller (1776) was perhaps the first author who called special attention to them. He de-

* I have purposely substituted the term "algae" for the term "gonidia." Gonidia and related terms as "gonimia," "gonidimia," etc., are meaningless in modern lichenology, and should therefore be rejected.

scribed them as "white circular depressions." This was about all that was known concerning these structures at that time. Acharius was the first to introduce the term cyphellae, which term has been retained up to the present. Since these organs are little known, it will be well to describe them more in detail.

The cyphellae occur almost exclusively in the genera *Sticta* and *Stictina* and are primarily breaks in the continuity of the lower cortical layer. The hyphae of the medullary layer immediately about the opening in the cortical layer divide more frequently, producing a dense net-work of hyphae or even a semicortical structure. As a rule, the cells of this secondary cyphellar formation extend in a direction at right angles to the outer surface; that is, they assume a suitable position for the conduction of food-substances. The margin of the primary cortical layer (the cortical layer of the thallus) is turned more or less outward. As a rule the algae of the algal layer immediately over the cyphellar opening multiply more rapidly, this causing them to accumulate at these areas.

Two kinds of cyphellae may be recognized. Form 1, as seen in *Stictina damaecornis*. The cyphellar depression is usually circular, concave inward, the margin of the cortex forming an outer constriction. The broken-down cortex of the thallus is replaced by the secondary semicortical formation of the medullary hyphae. Its outer surface is usually smooth, devoid of rhizoids, and generally of a paler color than the primary cortical tissue. They are irregularly distributed over the elevated portions of the lower surface of the thallus; none ever occur in the grooves. They appear first in the older portions of the thallus. In form they are quite constant, in size they decrease toward the younger portion of the thallus.

Form 2, as seen in the majority of *Stictas* and *Stictinas*. It is much more common and differs from the former in the absence of the formation of a secondary semicortical cyphellar covering. Instead of a depression as in the former case, there is usually a protrusion of the densely interwoven network of medullary hyphae. Their form is usually less regular. Their position and arrangement is the same as in the first form.

Both forms of cyphellae are sufficiently large to be seen by

the naked eye. No cyphellae occur near the actively growing tip of the thallus.

Acharius applied the term cyphellae to the form first described. Those of the second form he considered to be soredia. Nylander retained the name cyphellae for the first form. The second form he designated as *psuedocyphellae.* There is no morphological or physiological reason why the latter should be designated as "false." Indeed it were more consistent to designate the first form as false since they are of less frequent occurrence. Stitzenberger* retains Nylander's distinction into true and false cyphellae and further subdivides them as to color into white and yellow. This subdivision seems to be valueless, since their color depends upon the color of the medullary hyphae. Stitzenberger considers them of special importance in his classification of the Stictei. I am, however, opposed to adopting as primary, morphological characters whose physiology is unexplained.

Having thus briefly treated of the morphology of cyphellae we will now refer to their probable physiological significance. As already stated, they very likely serve to admit air into the interior of the thallus. Some of the older lichenologists looked upon them as vegetative propagative organs, similar to the soredia. They are not soredia, since they usually contain no algae. That the second form may accidentally contain algae is possible, since we find occasional algae throughout the medullary layer. It is, however, unreasonable to suppose that they would normally contain algae, since their position is not suitable for the development of the symbiotic algae. From the nature of the cortical layers and the epidermis in the majority of Stictei, it is reasonable to assume that the cyphellae serve a function similar to that of the stomata of ordinary foliage leaves. That is, the cyphellae and breathing pores of lichens are functionally similar. If it is scientific to make any comparison of the morphology of lichens and phanerogams it may be stated that the cyphellae are analogous to lenticels.* The tissue which closes the opening in the lower cortical layer is the result of a special cambial or meristematic activity.

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* Stitzenberger, E. Die Gruebchenflechten (Stictei) und ihre geographische Verbreitung. Flora, 81: 88–150. 1895.

* This analogy was pointed out by Dr. Smith Ely Jelliffe at a recent meeting of the Torrey Botanical Club (November 5th).

There is still another adaptive structural feature in the thallus of many lichens, especially in the Stictei, which is of undoubted physiological importance. These lichens present a striking appearance by the numerous ridges and depressions on the upper surface of the thallus. Morphologically and physiologically the ridges are analagous to the vascular system in the true foliage leaves. On microscopic examination it is found that the majority of the medullary hyphae of the ridges extend parallel to the direction of the ridges. In this region the medullary layer is also considerably thickened. It is a structure specialized to conduct the products of assimilation. This wavy outline of the thallus also increases surface expansion, whereby assimilation is increased. Assimilation is most active in the depressed portions of the thallus, which also corresponds to the position of the cyphellae on the lower surface. Such a wavy arrangement of structures also serves a mechanical function; according to the principles of mechanics it affords a better support to the frequently very large thallus.

A Study of the Genus Galactia in North America.

By Anna Murray Vail.

The genus *Galactia* was established by Patrick Browne in Nat. Hist. Jamaica, 298. *pl. 32. f. 2.* 1756. It was based on the plant figured in the illustration, a species with the stamens of *Galactia* and the showy scarlet flowers of *Collaea*, which forms a connecting link between these two sections. Linnæus reduced the genus to *Clitoria*, describing the Jamaica plant under the name of *Clitoria Galactia.** Michaux in Fl. Bor. Am. 2: 61, revived the genus, with two North American species.

The following genera have been reduced to *Galactia:*

Odonia Bertol. Lucub. Herb. 35. 1822.

Sweetia DC. Mem. Leg. 358. 1823.

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* The synonymy of this species is as follows:

Galactia Galactia (L.).

Clitoria Galactia L. Sp. Pl. Ed. 2, 1026. 1763.

Galactia pendula Pers. Syn. 2: 302. 1807.

Illust. Lindl. Bot. Reg. *pl. 269.* 1818.